Chapter 3
Historical Background of Ecological Modelling and Its Importance for Modern Ecology

Broder Breckling, Fred Jopp, and Hauke Reuter

Abstract The chapter outlines major routes of development leading to the current spectrum of concepts and applications in ecological modelling. The field is closely linked to achievements in other sciences, in particular physics, numerics, computer science, and cross-disciplinary adoption of ideas. Ecological modelling emerged initially as a relatively homogeneous field and mainly employed differential equations which originated in classical mechanics. Quantitative ecological dynamics were initially described in a formal analogy to physical processes. In the last few decades, the methodological repertoire in ecological modelling was successively expanded. Nowadays, the whole range of quantitative methods available in numerical mathematics can be seen as a foundation for future model development in ecology. Some pioneers in the field are briefly introduced and their contributions linked to some of the mainstreams and sidelines of the state-of-the-art in ecological sciences. The overview provided here will not be able to provide historical completeness but attempts to facilitate an understanding of the origin of the major approaches presented in this book and how they obtained their role in current ecological modelling.

3.1 A Historical Journey: Mainstream and Sidelines of Model Development in Ecology

Science as a whole has and continues to undergo a long process of advancement. At each period, the current state-of-the-art also represents the background of expectations for how the domains of the unknown might be tackled and structured in the future. The state-of-the-art provides the vocabulary, the grammar, and the paradigms

B. Breckling (✉)
General and Theoretical Ecology, Center for Environmental Research and Sustainable Technology (UFT), University of Bremen, Leobener Street, 28359 Bremen, Germany
e-mail: broder@uni-bremen.de

F. Jopp et al. (eds.), *Modelling Complex Ecological Dynamics*,
DOI 10.1007/978-3-642-05029-9_3,

of world views. When looking back, it becomes apparent that the particular view of each development phase had the tendency to give rise to interesting extrapolations. The existing domains of the unknown get filled with structural analogies of what was known. To this day, existing knowledge creates expectations of what is to come, therefore, truly new knowledge is frequently surprising and controversial. In Italy, Galileo Galilei (1564–1642) established experimental investigations as a targeted approach on scientific questions. In France, René Descartes (1596–1650) provided an elaborated philosophical underpinning of science in a mechanistic world view. In Britain, Newton (1643–1727) formulated a synthesis that showed a validity of the same mechanic laws being applicable on the microscopic scale of the laboratory as well as on the macroscopic scale in astronomy. From 1751 onwards, the French encyclopaedists Denis Diderot (1713–1784), Jean Baptiste D'Alembert (1717–1783), and others attempted to turn a synopsis of science into an emancipatory power during the era of enlightenment. In the following time, science diversified methodologically. Thermodynamics, chemistry, statistical mathematics, and other fields rapidly progressed. In this concert, ecology arrived relatively late. The German chemist Justus von Liebig (1803–1873) had already established the use of synthetic fertilizer. Organic chemistry was advancing when Ernst Haeckel (1834–1919) coined the term "ecology" in 1868 in his book "General Morphology of Organisms" (1868). In 1935, when Tansley introduced the term "ecosystem", the very first modelling applications in ecology had just been developed. The starting of ecological modelling occurred during the 1920s. It is quite obvious that we do not report about a canonical field – there are lots of different opinions and views about modelling in ecology. So we just take a glimpse of a transient process, which is not only influenced by achievements arising in ecological science. Modelling techniques and their ecological applications emerge in an intense exchange with scientific advancement in other disciplines.

3.2 Ancestors of Ecological Modelling

Ecological modelling deals with the formalization of dynamic and complex interaction networks, how organisms relate with each other and with their environment. Modelling attempts to uncover implications of understandable relations that are not obvious at first glance when looking at the organisms and the locations where they occur. With model development we hope to identify concealed implications. We attempt to approximate and expand the margins, and the boundaries of what is intelligible. The new insight that a good model provides, goes beyond what can be concluded with direct observation, evaluation and interpretation.

Though the term ecology is relatively young, the assessment of natural processes is much older. We can find the precursors of ecological modelling in natural history and also in other disciplines.

Modelling as Derived from Physics: Ecology as Derived from Natural History

Physics had the role of the paradigmatic, standard-setting science. The establishment of the experimental method as a primary source of rational intelligence was established first for physical relations. Galilei and successors emphasized that a temporally limited experiment, well isolated from the context and carefully arranged, can stand as a prototype for a class of similar phenomena. Knowing one outcome informs about the entire field of identical settings. One case can stand for all – as long as standardization is adequate. This applied to inorganic material, i.e. *res extensa*, as Descartes put it. He exempted *res cogitans*, the domain of intelligence, where mechanistic paradigms would not hold in his opinion. Living beings – though usually considered as plain *res extensa* – posed difficulties to some degree. Discussions sparked about how far man and animals share certain properties, and how the human mind as a domain of free choice and brain as a domain of its physical substrate would relate. In neurology and brain research certain aspects of this controversy continue today (Maasen et al. 2003).

Studying the diversity of life and life forms was the domain of natural history (Mayr 1982). An early impetus of natural history was a theological interest to illustrate the richness of creation (natural theology, e.g. Paley 1803). Natural history was largely descriptive and quantification played a relatively marginal role. This line of tradition was influential in ecology. It remained meaningful and it caused scepticism towards quantitative "physicalistic" descriptions. The founder of ecology, Ernst Haeckel himself, did not emphasize the application of quantitative methods in ecology. He largely used conceptual approaches, verbal descriptions, and graphical representations. The initiative to look at quantitative relations of man and environment did not emerge in the context of natural history or ecology but in physics, in economics, and demography.

Malthus: Basic Ideas in Population Science

Robert Malthus (1766–1834) was one of the first to introduce quantitative considerations in the population context. He considered implications and determinants of the growth of human populations. Mainly operating from an economic perspective, his ideas had subsequent influence for ecological considerations. He linked the growth and well-being of the human population directly with a development of natural resources (Malthus 1798) (Fig. 3.1).

Later, Darwin (1809–1882) considered the malthusian ideas in his development of evolutionary theory. A key idea of Malthus was that population growth tends to exhibit self-similar characteristics: If each of the population member has the same chances of fertility in space and time, the involved growth processes tend to be exponential. With a constant rate of increase, exponential growth accelerates

Fig. 3.1 Robert Malthus
source: wikimedia commons

over time. On the other hand, Malthus argued, resource development would not proceed exponentially but follow a linear dynamic. Malthus saw the discrepancy between these two growth forms of arithmetic versus geometric growth as an inevitable source of tension and instability. This controversy substantially inspired the following scientific debate on well reasoned, quantitative considerations on the human use of natural resources. At that time, Malthus' major impact was not in the field of ecology as he worked in the newly developing field of political economics. Here, in the era of European imperialism, his ideas played an important role in the discussion about how to deal with scarce and limited resources (Claeys 2000).

Verhulst: Early Functional Generalizations

It did not take long until other, successively more elaborated functional forms to describe growth were provided. Pierre Francois Verhulst (1804–1849) (Fig. 3.2) was a Belgian mathematician, who sought a way to describe the modification of growth intensity under the conditions of limited resources. He found a rather simplistic form in 1838. His function is still widely used in ecological modelling under the name of logistic growth (see Chap. 6: Differential Equations (6.7)).

The growth process that this equation describes always tends towards an equilibrium. Interestingly, for quite a long time logistic growth was far less considered, compared to Malthus. It was largely forgotten until Raymond Pearl (1879–1940) rediscovered it when ecological modelling had made its first steps in the 1920s (Pearl 1925). This was when the relevance of quantitative considerations as a foundation of ecology became more and more potent (see Lotka and Volterra, below). In physics, chemistry and other fields of science, advancement had led to

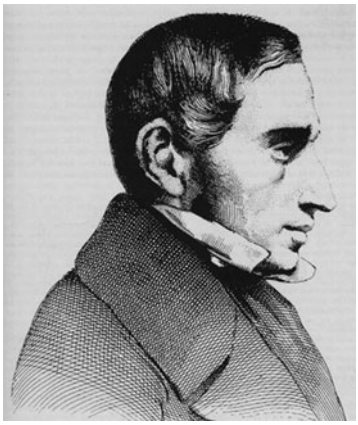

Fig. 3.2 Pierre Francois Verhulst
source: wikimedia commons

a well established mathematical underpinning and to the discovery of more and more quantitative relations. Ecology – terminologically existing as a sub-discipline of biology – was still largely dominated by qualitative assessment.

3.3 Founders of Ecological Modelling

In the first half of the twentieth century, Einstein's relativity theory of 1905 had been successively accepted in physics. Quantum theory was on the way, and David Hilbert discussed infinite dimensional vectors as mathematical objects. With some lag, the relevance of quantitative relations received attention in ecology as well. This started with quite elementary and simple contexts, which did not require elaborated mathematical forms. Differential equations, which describe the change of particular variables over time, played the leading role.

Lotka and Volterra: Setting the Stage for Network Approaches

Independent from each other, Alfred Lotka (1880–1949) and Vito Volterra (1860–1940) developed the same simplistic form to describe the interaction of a predator population and a prey population (Lotka 1925; Volterra 1926). The equations are explained in detail in Chap. 6. In the subsequent time, this model inspired innumerable variations, modifications, and adaptations to specific contexts. To this day, the original works of Lotka and Volterra are among the most frequently cited papers in ecological modelling. The Verhulst-equation, re-discovered by Pearl around the same time, helped to extend the functional repertoire usable in the equations. The Lotka–Volterra (LV) model describes the interaction

of two species in the most simplistic way. Actually, any real ecological context is by far more complex than two types of organisms interacting in a constant environment. Interestingly, in a metaphorical sense, it can be stated, that the LV-equations have the same role in ecology as Kepler's laws had in astronomy: the two-body problem can be mathematically solved. In isolation, the mutual gravitational impact of two objects is easy to describe in an equation. But when three or more mass points influence each other, it becomes very difficult to develop a valid model. The three-body problem requires numeric approximation and can be solved only in some special cases. In ecology, it was now possible to write down one, two, or a larger number of equations for the interaction of populations. But the equations could not be solved if their complexity was only a little bit higher than the LV-model. This may have been the reason why ecological modelling still played a peripheral role in the ecological science. This aspect changed with the extent that network interactions could be numerically managed.

von Bertalanffy: System Theoretic Foundation and Generalization

The Austrian biologist and philosopher Ludwig von Bertalanffy (1901–1972) (Fig. 3.3) played an important role in establishing and popularizing the systems perspective in biology in general, and influenced ecology (1949, see also 1969). He developed the concept of a flow equilibrium and emphasised the holistic approach. This encouraged to turn conceptual reasoning about the relations of interacting parts and the whole into practical research agendas. In his time, the transition was

Fig. 3.3 Ludwig von Bertalanffy (courtesy of Bertalanffy Center for the Study of Systems Science, W. Hofkirchner, Vienna http://www.bertalanffy.org)

made where network structures could not only be formulated but also iterated. This allowed to approximate the dynamic processes in complex networks. He, and the following colleagues were influential for network approaches to gain further roots in ecology.

Lindeman, EP and HT Odum, Waddington: Modelling and Ecological Application

There are many scientists who influenced the establishment of quantitative views in ecology. We select a few. Raymond Lindeman (1915–1942) (Fig. 3.4) pioneered the concept of trophic dynamics. In his 1942 work at the University of Minnesota (USA) he elaborated quantitative relations in an ecosystem context. At this time, he still met reservation whether this would bring ecological research forward.

For further description of his work: see Chap. 18 on trophic cascades. In the 1950s, Eugene Odum (1913–2002) published an influential textbook (1953), where he emphasized quantitative relations in a systems context as a means for ecosystem management. With this book, "modern ecology" reached the surface of the scientific mainstream. His brother Howard forwarded the idea to represent relevant relations in ecological systems using energy equivalents incorporated in biomass as a unifying measure. The energetic content of biomass could be used as a basis for homogeneous descriptions applicable for all ecosystem types. Paradigmatic in this context was the Silver Springs Ecosystem study (Odum 1957). Odum and colleagues refined their conceptional ideas in further studies (see Fig. 3.5). Though the concept is generalizable in a formal sense, as any change in ecological system has energetic implications, not all aspects were solved. This was because numerous factors influence the quantitative changes in energy transfer. E.g. limiting factors of

Fig. 3.4 Raymond Lindeman (by courtesy of University of Minnesota Archives)

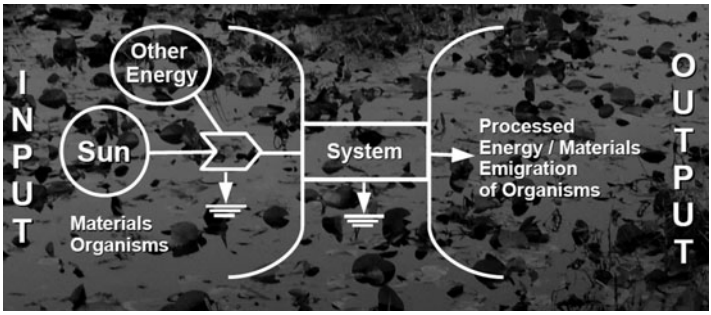

Fig. 3.5 Conceptional ecosystem model with input and output side following Patten (1978) and Odum (1997)

chemical nutrients, and information processing by the organisms. Systems ecology proceeded in a controversial way. The International Biological Programme (IBP), established in 1962, executed 1964–1974, was the first global attempt to provide a quantitative overview across different ecosystem types. The co-ordinator was C.H. Waddington (1905–1975). Representative ecosystems were identified and biotic inventories and quantitative trophic relations were investigated with a comparably large effort (Worthington 1975). For the first time, a large international effort was centred on ecosystems research including co-ordinated modelling efforts. Continuations of the research efforts provided model approaches that were quite important in the understanding of the forest decline, which was a large-scale phenomenon as a consequence of acidification of precipitation through industrial emissions during the 1970s and eighties (Bossel 1986, 1996).

Forrester, Meadows, Patten, Joergensen: Ecological Systems and Interdisciplinary Linkages

The systems approach has been continuously elaborated since the 1950s. Methods were developed that allowed to link knowledge from different disciplines in co-ordinated research frameworks. The interdisciplinary methods are described in further detail in Chap. 4. Origins were in systems philosophy (von Bertalanffy), and in industrial dynamics. Forrester (1961) developed a systems approach that he initially applied to understand complex matter flows in industry and the relating economic flows. The approach was subsequently generalized (Forrester 1969) and applied in a global environmental context (Meadows et al. 1972). Bernhard Patten (1976) exemplified the applicability for systems ecology. The strength of the approach was in facilitating an interdisciplinary understanding, to structure complex research tasks and to organize larger consortia of researchers contributing to an overall goal. With numerous works of Joergensen, e.g. his activity to establish the Journal *Ecological Modelling* in 1975, with the compilation of Textbooks (Joergensen 1986) and handbooks (e.g. Joergensen 1979), and the establishment

of the International Society for Ecological Modelling in 1975, the topic was fully established as a conceptionally and methodologically expanding science.

To meet the demands of empirical complexity, it became necessary to involve additional methods. Most of these additional methods were again imported from other disciplines and adapted to ecological requirements and then yielded the repertoire of modelling complex ecological dynamics.

3.4 Diversification and Diversifiers

During the 1980s it became apparent that homogeneous variables had a limited potential to fully capture the complexity of ecological relations. In particular, quantity–quality transitions and inhomogeneous temporal and spatial structures were difficult – at least inconvenient – to be captured in differential equation systems. Criticisms towards modelling as such (e.g. den Boer 1981) would be overcome when modelling methodologies diversified.

The Object Paradigm and Individual-Based Modelling

During the 1960's, Ole Johann Dahl (1931–2002) (Fig. 3.6) and Kristen Nygaard (Fig. 3.7) from the Norwegian Computer Centre in Oslo developed a computer language which went conceptually beyond the established so-called procedural approach: With SIMULA (SIMUlation LAnguage), extending ALGOL (ALGOrithmic Language) they introduced options that allowed a kind of self-structuring during programme execution (Dahl et al. 1968). Reference variables could point to particular addresses of the computer storage to indicate the location of complex data objects. These data objects could be created and deleted when running the programme and utilize references to each other that could be changed during execution. This yielded *object-oriented programming*, which became generally known in computer science with the SMALLTALK-80 programming language

Fig. 3.6 Ole-Jan Dahl, courtesy of Depart. of Informatics, University of Oslo

Fig. 3.7 Kristen Nygaard

with C++ and others during the late 1980s. These developments opened considerable new options in ecological modelling, since object orientation allowed a convenient linkage of structural and functional dynamics, which had been difficult to bring together. In both domains, changes could be synchronously represented – by changing the object structure together with the values of the variables stored in the objects (Fig. 3.8). One of the first, who understood the importance for ecology was Heinrich Kaiser in Aachen (Germany). He used the approach for the development of individual-based models (Kaiser 1976, 1979). A Pioneer in the field was also Paulien Hogeweg in Utrecht (The Netherlands, see Hogeweg and Hesper 1979, 1983). The individual-based approach offered far more options to synchronously represent variability in physiological states of organisms, usage of their behavioural repertoire and responses to time variant structural environmental pattern (Huston et al. 1988; Judson 1994).

The Self-Organization Paradigm

The self-organization paradigm became influential in ecology at about the same time as the individual-based modelling approach. It emerged in the context of physics (Haken 1977), thermodynamics (Glansdorff and Prigogine 1971), and systems theory. The proponents of the self-organization approach argued the following: Science as a whole is grounded on the principle of causality. Any change that occurs has an antecedent cause. Same settings, same causes always produce the same results. In this way, causes and effects were traditionally segregated. What happens if they interact in large numbers and complex networks? With the availability of automated calculation potential, non-trivial effects were discovered in loop-structures where interaction results served as a new input (the effect becomes a new cause that feeds back in iterative cycles). In feedback structures, non-trivial states can emerge that cannot be reduced to plain external impact. Systems can self-generate

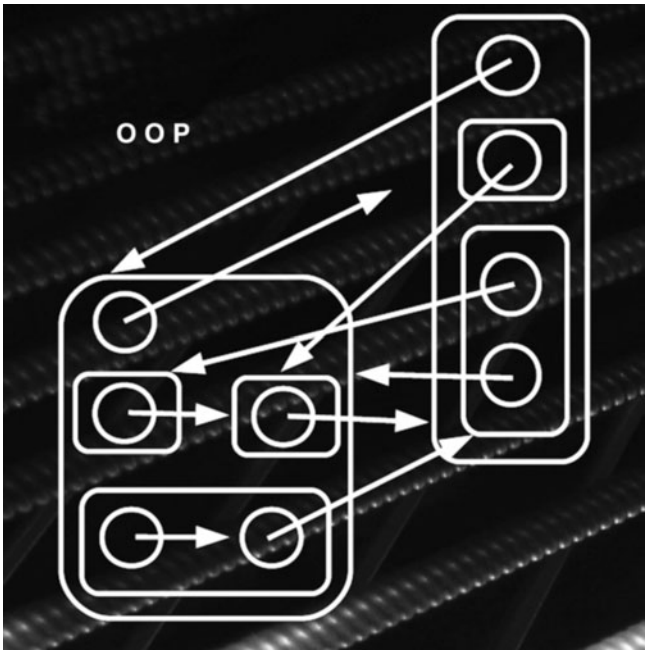

Fig. 3.8 Scheme of an object-oriented programme during execution state. The objects are using pointers to access each other (see Chap. 12)

complexity. This became a very influential idea for interdisciplinary exchange (Jantsch 1980; Prigogine and Stengers 1984). In parallel to ecology, the self-organization discourse influenced biology as a whole, as well as the social sciences, psychology, and other fields of science and philosophy. The Santa Fe Institute (New Mexico, USA) developed the research agenda of Artificial life. Here, formal descriptions of how living entities self-organize were used to study the potential to simulate properties of living systems using physical substrates (Langton 1994). Frequently, object structures were used, but also other approaches like Cellular Automata (see Chap. 8), which had received relevant applications in physics, and thermodynamics. Moreover, fractals were used (Mandelbrot 1982) and new developments in the theory of dynamic systems (Peitgen 1992), all of which had become more widely recognized during the 1980s and 1990s.

3.5 Anything Goes: The Diversity of a Post-Modern Ecology

Where are we now? Ecological modelling is a well established discipline. It is recognized that the understanding of complex phenomena requires modelling and that formal approaches can to a considerable extent capture the quantitative and qualitative understanding we have about biological systems and their environmental interactions. From model representations, we also know that marginal shifts can

be amplified and alter directions of development, which allows qualitative understanding but limits prognostic potential. It is clear meanwhile, that not a single methodological approach is equally suitable for all questions and problems. This confronts ecologists with the requirement to select appropriate approaches. Which one to chose depends on the problem to be solved. Nowadays, methods from many different sources are adapted if they are suitable for ecological modelling purposes.

How else could we discover activity pattern and behaviour of marine animals except by combining radio tracking, remote sensing and other technical devices with data evaluation facilities to come up with object oriented behavioural models (see Chap. 12)? How else could we come up with realistic plant shape models without using graphical iteration (see Chap. 11)? How else could we gain an integrated picture of landscape dynamics and how it alters the living conditions for protected organisms, if not using a larger set of methods in parallel with network-like connections of mutual input (see Chap. 21)? We use differential equations, matrix models, individual-based descriptions – as presented in the different chapters of this book as single approaches – or when it is needed, various model components will be coupled together (see Chaps. 20 to 22).

Promising approaches are very welcome for ecological application when it helps and inspires the understanding of organisms and their relations among each other and their environments. Regardless of the currently available, amazing supply of modelling techniques and methods, we ecologists should always stay focussed on one thing: to develop our own model.